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Landscape-Level Effects on Habitat Use, Nesting Success, and Brood Parasitism in the Southwestern Willow Flycatcher

LANDSCAPE-LEVEL EFFECTS ON HABITAT USE, NESTING SUCCESS, AND BROOD PARASITISM IN THE SOUTHWESTERN WILLOW FLYCATCHER

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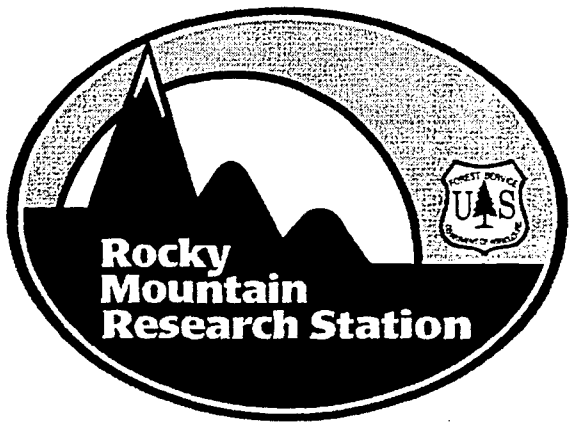


INTRODUCTION

In the past decade, avian ecologists increasingly have focused on ecosystem processes and patterns at spatial scales larger than the nest site or territory, such as the patch or landscape scale (Freemark et al. 1995). In particular, scientists concerned about declines in Neotropical bird species have examined changes in landscape characteristics to explain those declines (Robinson et al. 1995, Askins 1995). Almost all of this work has been conducted in the eastern half of North America, where a majority of the avifauna is adapted to forest interior conditions. There, forest fragmentation has caused these forest interior bird species to increasingly overlap with predators and brood parasites typical of open areas and edges, often with disastrous consequences (Paton 1994, Danielson et al. 1997). This is the so-called edge effect. Moreover, these effects decrease with distance from edge, such that larger patches provide better habitat than smaller ones.

In contrast, in the western parts of North America, contiguous closed-canopy forest is uncommon, being found primarily in high-elevation montane areas. Much of the region supports non-forested habitats such as grasslands, shrublands, and desert. Within these non-forested habitats, riparian systems often support narrow, linear corridors of close-canopied woodland, which support a rich and distinct avian community (Knopf et al. 1988). It remains unknown if the negative impacts of forest fragmentation and edge effects so well documented in the East are equally prevalent in these lower-elevation western habitats. One study in Montana suggests not (Tewksbury et al. 1998).

In the Southwest, riparian ecosystems have been severely degraded and fragmented by as much as 90% (Knopf et al. 1988). However, these riparian systems are highly dynamic in nature, resulting in a natural pattern of fragmentation (Szaro 1989). The Southwestern race of the Willow Flycatcher (*Empidonax traillii extimus*) is a critically endangered Neotropical migrant bird that breeds exclusively in densely vegetated riparian areas in the region. Approximately 600 pairs were known to exist in 1999, with more than a third of those in the upper Gila River Valley in New Mexico (Marshall 2000). It is currently considered the top priority species for US Fish and Wildlife Service Region 2. Within its range, many apparently suitable habitat patches (based on vegetation composition and structure) remain unoccupied. Among occupied patches, rates of nesting success and cowbird parasitism vary greatly. While

several studies have now examined nesting success, parasitism, and microhabitat preferences within a single site (e.g., Whitfield 1990, Sogge et al. 1997a, Stoleson et al. 1998, Stoleson and Finch 1999a), none has addressed landscape-level effects on habitat occupation and nesting success. Such landscape-level effects on the flycatcher have been identified as a top research priority (Stoleson et al. 2000).

In this study, we examine landscape-level correlates of patterns of habitat use, patch occupancy, nesting success, and rates of cowbird parasitism on Southwestern Willow Flycatchers in the Cliff-Gila Valley, NM. Specifically, we address several questions: (1) what constitutes Willow Flycatcher habitat at the patch level? (2) what patch and landscape-level factors affect Willow Flycatcher nest success and brood parasitism? (3) are birds of Southwestern riparian woodlands subject to the same negative impacts of edge and patch size as are forest birds in more mesic regions?

METHODS

Study area. — The Cliff-Gila Valley of Grant County, NM, comprises a broad floodplain of the Gila River, beginning near its confluence with Mogollon Creek and extending south-southwest toward the Burro Mountains. The study site contains a mosaic of riparian habitats of varying ages, sizes, composition, and topography, spread along approximately 18 km of river. This study was conducted from just below the US Route 180 bridge upstream to the confluence of Mogollon Creek and the Gila River, a linear distance of 9 km. In addition, flycatchers were studied in a portion of the next valley downstream in the Gila River Bird Habitat Management Area, a riparian restoration project comprising lands of the Gila National Forest and Pacific-Western Land Company, located some 8 km downstream of the Route 180 bridge.

Most of the upper Gila Valley consists of irrigated and non-irrigated pastures used for livestock grazing and hay farming. Elevations range from 1350 to 1420 m. The Gila River and nearby earthen irrigation ditches are lined with riparian woodland patches of various ages and composition. Most patches support a mature woodland (>25 m canopy) of Fremont cottonwood (*Populus fremontii*), with a subcanopy of mixed deciduous trees including box elder (*Acer negundo*), Goodding's willow *(Salix gooddingii*), velvet ash (*Fraxinus velutinus*), Arizona walnut (*Juglans major*), Arizona sycamore (*Platanus wrightii*), Arizona alder (*Alnus*

oblongifolia) and Russian olive (*Elaeagnus angustifolia*). The understory is composed of shrubs including three-leaf sumac (*Rhus trilobata*), false indigo (*Amorpha fruticosa*), New Mexico olive (*Forestieria neomexicana*), forbs, and grasses. Fewer patches support a shrubby, early successional growth of seepwillow (*Baccharis glutinosa*), coyote and bluestem willows (*Salix exigua* and *S. irrorata*), and saplings of the species mentioned above. Most habitat patches are less than 5 ha in area.

We identified and included in our analyses 39 discrete woodland patches in the Cliff-Gila Valley (Fig. 1). We limited our focus to those patches that might be considered potential flycatcher habitat according to published descriptions (Stoleson and Finch 1999a, b, Sogge and Marshall 2000). Patches included were (1) well within the floodplain and so mesic enough to qualify as habitat, (2) wide enough (>10 m average width), and (3) of sufficient age and stature to provide adequate structure. We did not include any of the numerous very small (< 0.3 ha) patches or young regeneration of coyote willow and seepwillow, as flycatchers in this area do not appear to use them regardless of landscape features (Stoleson and Finch, unpublished data).

Vegetation and Landscape Measurements. — Within each patch, vegetation was sampled systematically starting from a randomly-chosen point, using a modified BBIRD methodology (Martin et al. 1997). Sampling points were established spaced 50 to 100 m apart and at least 10 m from habitat edges. The number of sample points per patch varied with patch size and shape. Vegetation characteristics measured at each point included stem counts for trees (within 8 m of point) and shrubs (within 4 m of point) by size class and species; basal area by species; average canopy height, and canopy cover. Canopy cover was measured using hemispherical densiometers; sample point values were the average measurements at the sample point and at 4 and 8 m in reach of the cardinal directions from the sample point. Canopy heights were measured using hand-held clinometers. For each vegetation variable, we calculated patch averages and standard deviations (as a measure of homogeneity within patches).

Locations and dimensions of riparian patches were calculated using a combination of GPS (Global Positioning System) measurements and photointerpretation of digitized aerial photos provided by the Gila National Forest. This area turned out to be one of the very few remaining in the country without registered digital orthoquads yet available; therefore, we were obliged to acquire basic spatial data in the field. For each riparian patch, we determined patch

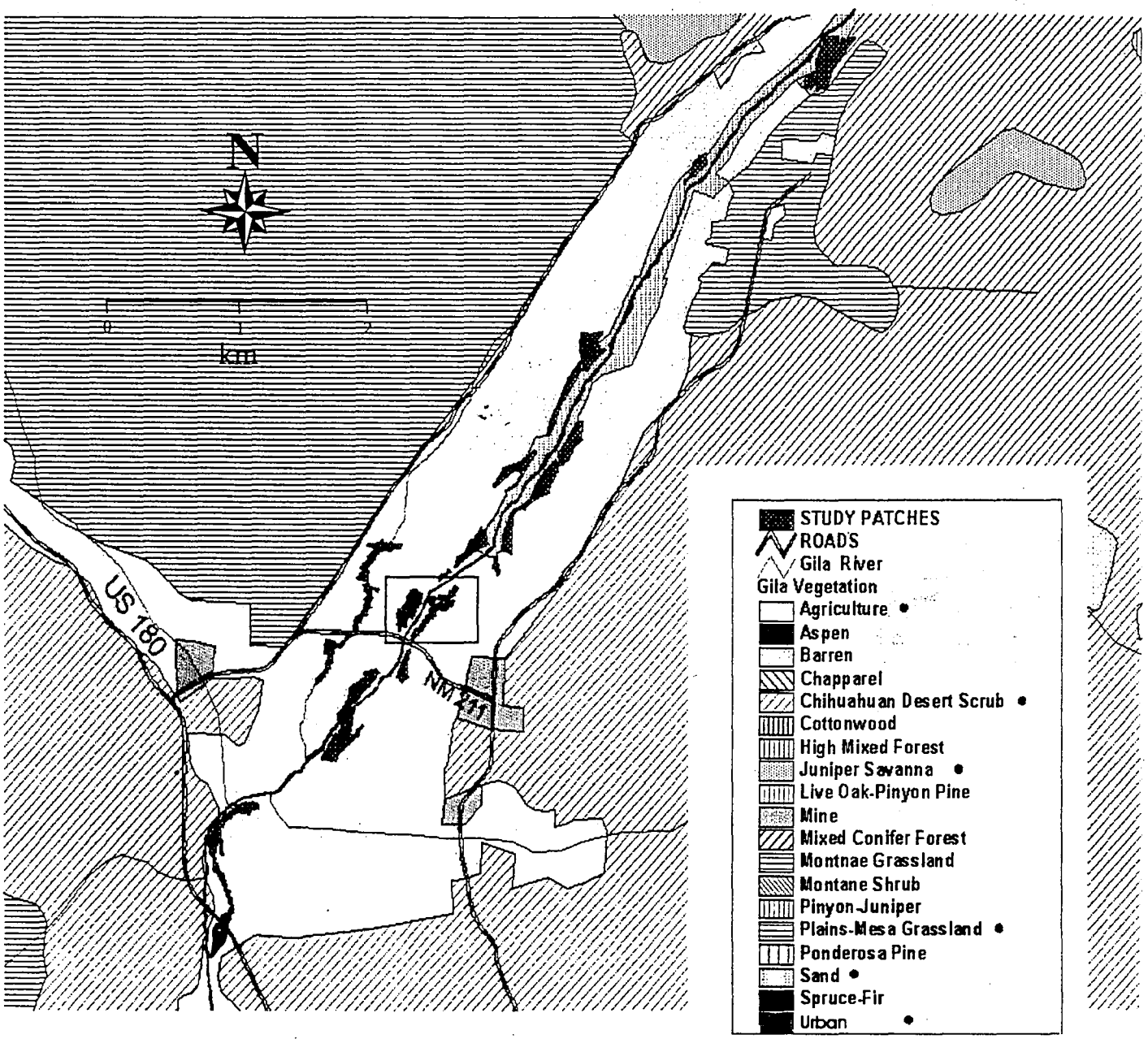


Figure 1: Arrangement of a sample of study patches (in green) in the Cliff-Gila valley, New Mexico, including habitat types. Inset indicates area shown in Fig. 2.

area (ha), average and minimum patch width (m), patch length (m; parallel to river course), proximity to water (m), proximity to river (m), proximity to nearest patch (m), proximity to nearest occupied patch (m), proximity to nearest roads (m), width of floodplain (m, perpendicular to river course), and proximity to nearest upland (Fig. 2). From these values, we calculated ratios of length to width, and perimeter to area, as measures of proportion of edge (Freemark et al. 1995). We determined the grazing status of each patch, which was entered into analyses as a categorical variable (grazed vs. ungrazed). Variables used in subsequent analyses are listed in Table 1.

Nest monitoring. — Nest searches were conducted on a daily basis in patches from 1997 through 2000. Nests were monitored every 3-7 days, following a modified version of proposed protocols suggested by the Arizona Game and Fish Department (Rourke et al. 1999). Nest contents were observed using pole-mounted mirrors or videocameras, or 15X spotting scopes. Nests that were abandoned or destroyed were examined for evidence (e.g., cowbird eggs, mammal hairs) to ascertain causes of nest failure. We considered a nest successful if: (1) parent birds were observed feeding one or more fledged young; (2) parent birds behaved as if dependent young were nearby when the nest was empty (defensive or agitated behavior near nest); or (3) nestlings were in the nest within one or two days of the estimated fledge date. We considered a nest failed if: (1) nest contents disappeared before fledging of young was possible, assuming 10-12 d required for fledging (depredation), (2) the nest contained no Willow Flycatcher young but contained cowbird eggs or chicks (parasitized), or (3) the nest was deserted after eggs had been laid.

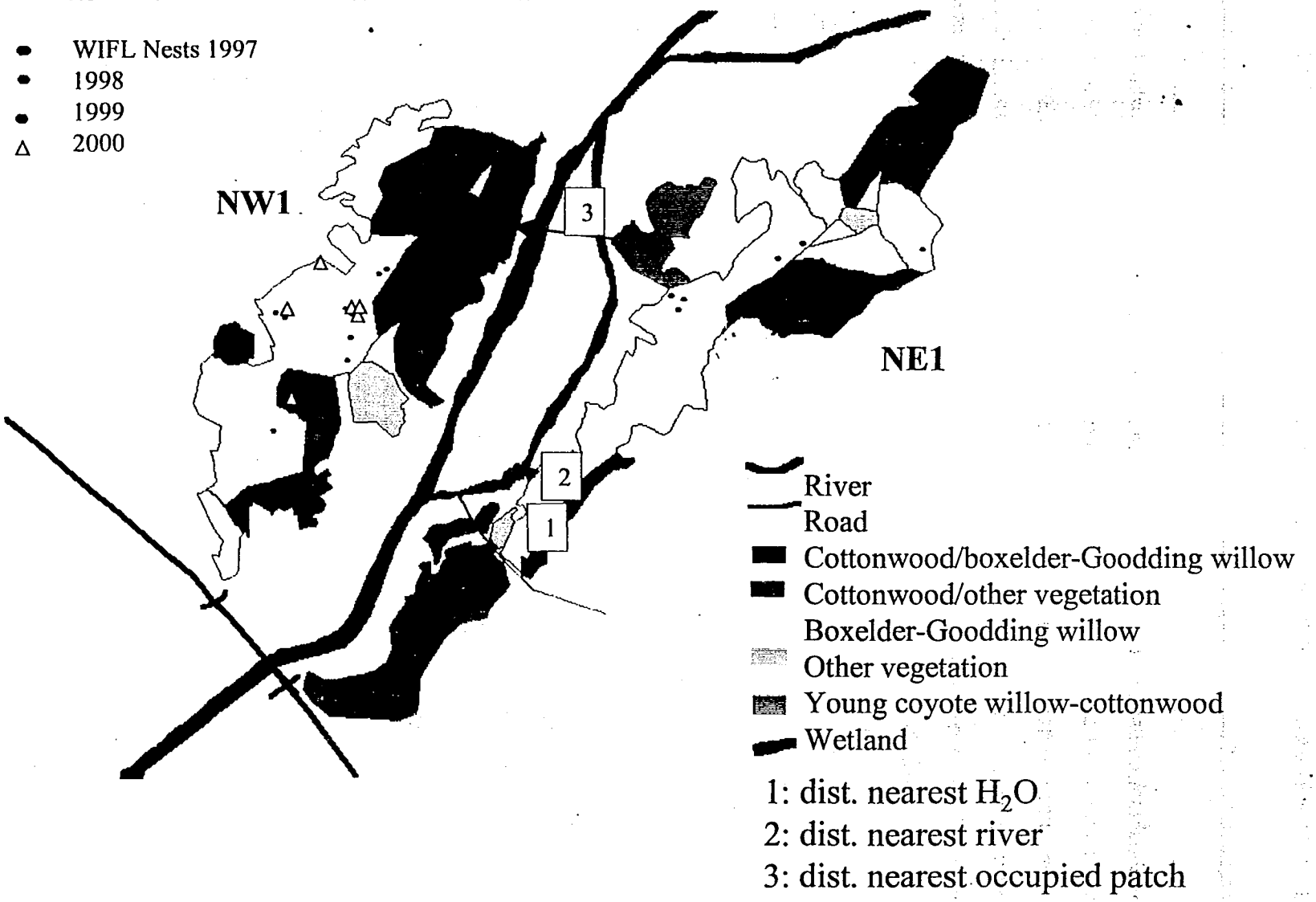
Analyses

We used nesting data from 1997-2000 to calculate patch-wise averages of flycatcher nesting success and rates of cowbird parasitism. Flycatcher population levels fluctuated among years, but proportions of the total found within each patch remained approximately constant each year. For analyses, we therefore used density estimates based on 1999 data only. All means are reported $\pm$ standard deviations.

Table 1. Landscape and habitat variables used in analyses

VARIABLE	DESCRIPTION
Patch size/shape	
AREA	Total area of patch, in hectares
LENGTH	Length of patch along axis parallel to river, in meters
AVEWIDTH	Average width of patch along axis perpendicular to river, in meters
LENGTH/WIDTH	Ratio of patch length to width
PERIMETER/AREA	Ratio of patch perimeter to area
Patch vegetation characteristics	
CANCVRave	Average % canopy cover in patch
CANCVRsd	Standard deviation of % canopy cover among sample points in patch
CANHTave	Average canopy height in patch, in meters
CANHTsd	Standard deviation of canopy heights among sample points in patch
SHRUBave	Average number of stems of shrubs and saplings per sample point
SHRUBsd	Standard deviation of shrub counts among sample points in patch
TREESave	Average number of stems of trees (≥10 cm dia.) per sample point
TREESsd	Standard deviation of tree counts among sample points in patch
Stems10-30	Average count of trees in 10 – 30 cm dia. size class per sample point
Stems30-50	Average count of trees in 30 – 50 cm dia. size class per sample point
Stems50-70	Average count of trees in 50 – 70 cm dia. size class per sample point
Stems70+	Average count of trees in 70+ cm dia. size class per sample point
%BOX	Percentage of woody stems in patch that are boxelder (*Acer negundo*)
%SALIX	Percentage of woody stems in patch that are willow (*Salix* spp.)
BASALAREAave	Average estimated basal area per sample point, in meter^2
BASALAREAsd	Standard deviation of est. basal area among sample points in patch
Patch position in landscape	
DistH20	Minimum distance to nearest water of any type, in meters
DistRIVER	Minimum distance to surface water of Gila River, in meters
DistNEAREST	Minimum distance to next nearest patch, in meters
DistOCCUP	Minimum distance to nearest patch occupied by flycatchers, in meters
FLOODPLAIN	Distance across floodplain perpendicular to flow of river, as measured at midpoint of patch, in meters
UPLAND	Minimum distance to closest upland/floodplain interface, in meters
DistROAD	Minimum distance to nearest road, in meters

Figure 2: Example of Willow Flycatcher nest placement within patches, showing distance to water, river, and next occupied patch. Note concentration of nests in box elder-dominated microhabitats.



Correlates of Patch Occupancy. -- To assess landscape correlates of patch occupancy, we first compared occupied and unoccupied patches for each numerical variable using univariate t-tests. We included all numerical and categorical landscape variables that differed significantly (at $p < 0.10$) between occupied and unoccupied patches in a step-wise logistic regression using patch occupancy as the dependent variable (Trexler and Travis 1993). We used a value of $p \leq 0.05$ to enter and 0.10 to remove individual variables from the model. We chose the most parsimonious among models with equal numbers of parameters using Akaike's Information Criterion (AIC), and we used Likelihood-Ratio Chi-square to test for significant effects between nested logistic regression models (Anderson et al. 2000).

Correlates of Flycatcher Density, Nest Success, and Brood Parasitism. -- We determined the correlation of each numerical landscape variable to the target variable using bivariate linear regressions. All numerical landscape variables that differed significantly (at $p < 0.10$) were included in a step-wise multiple regression, using $p \leq 0.05$ to enter and 0.10 to remove. We also compared the means of target variables between grazed and ungrazed patches using t-tests. To assess any impacts of grazing as practiced at this site, we tested whether nest success and brood parasitism were density dependent by regressing the target variable against population density.

RESULTS

Patch descriptions. – The 39 woodland patches included in analyses ranged from 0.38 to 11.8 ha in size. All patches were located in an extensively agricultural valley, although the management of some portions was recently (since 1990) changed to pure preservation (properties of The Nature Conservancy and the Gila National Forest). Most of the patches were located on a working cattle ranch; many of these patches had cattle excluded by fences, however. Overall, 18 of 39 patches were grazed, primarily in fall and winter only. We found no other variation in land use or other characteristics of the inter-patch matrix (e.g., stream gradient, slope).

Of the 39 study patches, 27 supported breeding Willow Flycatchers in 1999. Flycatcher densities varied greatly among occupied patches, and ranged from 0.25 to 10.3 pairs/ha. Average nest success within patches (from nests monitored 1997- 2000) also varied greatly, from 0% to 100% successful (mean = 0.51 $\pm$ 0.24, n = 392 nests of known outcome). Brood

parasitism within occupied patches varied from 0% to 100%, with a mean of 19.9 ± 29.9% (n = 222 nests of known parasitism status). Patches with very high or very low rates for either parameter had very small sample sizes (< 5) of flycatcher nests.

Landscape correlates of Flycatcher occupancy

Land use. – We found no evidence that grazing within a patch discouraged flycatchers from occupying that patch. Flycatchers were found in a significantly greater portion of the grazed patches than the ungrazed patches (87.5 vs. 52.4%, respectively; $\chi^2 = 6.5$, df = 1, $p = 0.011$).

Univariate regressions. – We compared each landscape variable between patches that were occupied and those that were unoccupied by Willow Flycatchers. Six variables differed significantly ($p \leq 0.05$) between occupied and unoccupied patches (Table 2). Patches with flycatchers averaged larger in area, greater in length, had lower variation in the numbers of shrubs, a higher percentage of boxelder, were closer to water, and closer to the next nearest patch, than were patches without flycatchers. An additional four variables showed trends towards differences between the two patch types ($0.05 < p \leq 0.10$). Occupied patches tended to have a greater length-to-width ratio and a lower perimeter-to-area ratio, a lower percentage of woody stems that were willow, and a broader floodplain than unoccupied patches.

Logistic regression model. – We used six of the variables found to have significant or near-significant differences above in a logistic regression analysis. Since all of the variables describing patch size or shape were highly correlated with each other (all $r > 0.5$, $p < 0.05$), we used only AREA, with the greatest p-value, in our analysis to avoid problems associated with collinearity of variables. Similarly, since the percentages of woody stems that were boxelder and willow were necessarily inversely correlated, we used only boxelder in our analyses.

The best logistic regression model, as determined by AIC, identified three variables as significant predictors of patch occupancy by Willow Flycatchers. These variables were percent of stems that were boxelder (%BOX), the distance to the nearest patch (DistNEAREST), and the standard deviation of shrub counts (SHRUBsd). This model successfully classified 96.0% of occupied patches, 77.8% of unoccupied patches, and 91.2% of patches overall. The beta

coefficients indicate that patches were increasingly more likely to be occupied with (1) increasing proportion of boxelder, (2) decreasing distance to nearest patch, and (3) decreasing variation in the number of shrubs among points within the patch (Table 3).

Table 2. Comparisons of landscape variables between patches occupied ($n = 27$) and not occupied ($n = 12$) by Willow Flycatchers. Significant p values (≤ 0.05) are indicated in bold.

Variable	Mean ± SD		t	df	p
	occupied	unoccupied			
AREA (ha)	4.30 ± 2.77	2.07 ± 1.36	-3.38	36.5	**0.002**
LENGTH (m)	507.71 ± 300.17	346.52 ± 134.49	-2.32	36.97	**0.026**
AVEWIDTH (m)	75.08 ± 43.34	70.39 ± 35.90	-0.33	37	0.75
LENGTH/WIDTH	8.16 ± 6.27	5.62 ± 2.43	-1.82	36.64	0.077
PERIMETER/AREA	355.41 ± 224.32	501.91 ± 220.91	1.77	35	0.085
CANCVRave (%)	83.59 ± 8.99	77.13 ± 19.20	-0.97	9.25	0.36
CANCVRsd	8.56 ± 3.89	14.32 ± 12.43	1.37	8.57	0.21
CANHTave (m)	14.98 ± 4.71	15.22 ± 7.58	0.12	36	0.91
CANHTsd	6.13 ± 3.06	5.05 ± 2.66	-0.94	32	0.35
SHRUBave (count)	28.30 ± 12.93	29.53 ± 17.60	0.24	36	0.81
SHRUBsd	14.57 ± 5.92	20.34 ± 5.47	2.56	32	**0.016**
TREESave (count)	10.02 ± 4.72	12.22 ± 7.85	1.01	33	0.32
TREESsd	5.22 ± 2.85	5.83 ± 3.78	0.50	32	0.62
Stems10-30 (count)	8.25 ± 4.80	10.19 ± 7.69	0.89	33	0.41
Stems30-50 (count)	0.97 ± 0.55	1.21 ± 1.14	0.60	9.31	0.56
Stems50-70 (count)	0.30 ± 0.30	0.39 ± 0.60	0.44	9.41	0.67
Stems70+ (count)	0.49 ± 0.58	0.43 ± 0.69	-0.27	33	0.79
%BOX	41.47 ± 28.67	8.87 ± 17.06	-4.41	33.57	**>0.001**
%SALIX	24.75 ± 21.83	40.31 ± 25.19	1.96	37	0.058
BASALAREAave (m^2)	418.37 ± 169.41	494.04 ± 275.98	0.77	10.17	0.46
BASALAREAsd	224.13 ± 119.13	237.76 ± 97.91	0.31	32	0.76
DistH20 (m)	3.74 ± 8.57	26.11 ± 33.58	2.28	11.64	**0.043**
DistRIVER (m)	64.24 ± 103.12	41.62 ± 42.82	-0.97	36.94	0.34
DistNEAREST (m)	174.57 ± 223.50	332.09 ± 221.62	2.04	37	**0.049**
DistOCCUP (m)	323.76 ± 660.96	792.73 ± 1121.34	1.64	37	0.110
FLOODPLAIN (m)	4256.43 ± 1764.87	3003.07 ± 1873.63	-2.01	37	0.052
UPLAND (m)	1160.12 ± 797.67	896.28 ± 805.90	-0.95	37	0.348
DistROAD (m)	1212.50 ± 740.26	1149.81 ± 876.80	-0.23	37	0.819

Table 3. Landscape variables found to be significant ($p < 0.10$) predictors of patch occupancy by Southwestern Willow Flycatchers, based on a stepwise logistic regression.

Variable	β coefficient	S.E.	Wald χ^2	df	p
%BOX	0.211	0.123	2.951	1	0.086
DistNEAREST	-0.016	0.010	2.635	1	0.105
SHRUBSsd	-0.496	0.259	3.674	1	0.055
CONSTANT	9.190	4.558	4.066	1	0.044

Landscape Correlates of Flycatcher Density

Land use. – Grazing appeared to have a significant effect on flycatcher densities. Grazed patches supported significantly higher densities (2.51 ± 2.70 pairs/ ha) than did ungrazed patches (0.98 ± 1.94 pairs/ha; $t = 2.05$, df = 37, $p = 0.047$).

Bivariate correlations. – We found only one landscape variable, percent of boxelder, was significantly correlated with flycatcher density. The density of flycatchers increased with increasing percentage of boxelder within patches. A second variable, width of floodplain, showed a nearly significant positive correlation with density, suggesting that the broader the floodplain, the higher the density of flycatchers.

Mutiple regression analysis. – The stepwise multiple regression analysis also revealed only boxelder to be a significant predictor of flycatcher density; density increased with increasing percentage of boxelder ($r^2 = 0.14$, $F_{1,29} = 4.85$, $p = 0.036$). As indicated by the r^2 value, this variable explained less than 15% of the variation in density among patches. There seemed to be no significant interaction effects in this data set.

Landscape Correlates of Flycatcher nest success

Population density. – Average rates of nest success within patches were not correlated with the density of flycatchers within those patches ($r^2 = 0.002, p = 0.84$). Thus, nest success does not appear to be density-dependent in this population.

Land use. – We found no detectable impact of grazing on flycatcher nest success. Occupied patches that were grazed ($n = 15$) had a similar overall rate of nest success (0.56) as patches that were excluded from grazing (0.45; $n = 12$; $t = -1.1$, df = 25, $p = 0.28$).

Bivariate correlations. -- Six variables were significantly correlated with average patch-wise nest success. Average rates of nest success increased with decreasing variation in canopy cover, and with increasing average canopy cover, average canopy height, numbers of woody stems in the 30-50 cm DBH and 70+ cm DBH size classes, and with increasing distance from nearest occupied patch (Table 5). Two additional variables showed not-quite-significant trends: nest success increased with decreasing variation in tree counts, and with increasing percent of stems that were boxelder.

Table 4. Bivariate correlations of landscape variables on average patch-wise density of Willow Flycatchers.

VARIABLE	Pearson *r*	*p*
AREA (ha)	0.023	0.89
LENGTH (m)	0.057	0.73
AVEWIDTH (m)	0.074	0.66
LENGTH/WIDTH	0.023	0.89
PERIMETER/AREA	0.010	0.95
CANCVRave (%)	0.069	0.69
CANCVRsd	0.093	0.60
CANHTave (m)	0.054	0.75
CANHTsd	0.098	0.58
SHRUBave (count)	0.11	0.52
SHRUBsd	0.089	0.62
TREESave (count)	0.16	0.37
TREESsd	0.092	0.61
Stems10-30 (count)	0.14	0.41
Stems30-50 (count)	0.042	0.81
Stems50-70 (count)	0.086	0.62
Stems70+ (count)	0.025	0.89
%BOX	0.44	**0.006**
%SALIX	0.19	0.24
BASALAREAave (m^2)	0.16	0.35
BASALAREAsd	0.13	0.48
DistH20 (m)	0.15	0.37
DistRIVER (m)	0.068	0.68
DistNEAREST (m)	0.25	0.12
DistOCCUP (m)	0.23	0.17
FLOODPLAIN (m)	0.28	0.080
UPLAND (m)	0.30	0.067
DistROAD (m)	0.071	0.67

Multiple regression analysis. – Five variables were found to be significant predictors of flycatcher nest success (Table 6). Oddly, only one variable identified as a significant predictor by the multiple regression analysis (CANCVRsd) showed a significant correlation with nest success in the univariate regression analyses. Nest success increased with increasing average basal area, and with decreasing width of floodplain, patch area, total number of stems in the 10-30 cm DBH size class, and variation in canopy cover. According to the multiple regression equation, these six variables explained 84% of the variation in nest success among patches ($r^2 = 0.84$, $F_{5,19} = 19.98$, $p < 0.001$).

Table 5. Bivariate correlations of landscape variables with average patch-wise nest success in Willow Flycatchers

VARIABLE	Pearson *r*	*p*
AREA (ha)	0.26	0.19
LENGTH (m)	0.18	0.36
AVEWIDTH (m)	0.17	0.41
LENGTH/WIDTH	0.10	0.61
PERIMETER/AREA	0.043	0.83
CANCVRave (%)	0.50	**0.010**
CANCVRsd	-0.56	**0.004**
CANHTave (m)	0.56	**0.003**
CANHTsd	0.33	0.10
SHRUBave (count)	0.27	0.19
SHRUBsd	0.28	0.18
TREESave (count)	0.059	0.78
TREESsd	-0.35	0.085
Stems10-30 (count)	-0.070	0.73
Stems30-50 (count)	0.46	**0.019**
Stems50-70 (count)	0.31	0.12
Stems70+ (count)	0.45	**0.023**
%BOX	0.37	0.057
%SALIX	-0.001	0.99
BASALAREAave (m^2)	0.28	0.17
BASALAREAsd	-0.031	0.89
DistH20 (m)	0.12	0.55
DistRIVER (m)	-0.22	0.27
DistNEAREST (m)	0.027	0.89
DistOCCUP (m)	0.39	**0.042**
FLOODPLAIN (m)	-0.062	0.76
UPLAND (m)	-0.062	0.76
DistROAD (m)	0.084	0.68

Landscape correlates of brood parasitism on Willow Flycatchers

Population density. – Average rates of brood parasitism within occupied patches were not correlated with the density of flycatchers within those patches ($r^2 = 0.002$, $p = 0.82$). Thus, brood parasitism does not appear to be density-dependent in this population.

Land use. – Brood parasitism within a patch was not significantly affected by grazing status of the patch. Average patch-wise parasitism rates did not differ between grazed (20.7 ± 29.3%) and ungrazed patches (18.8 + 31.9%; $t = 0.16$, df = 25, $p = 0.88$).

Table 6. Variables included in a linear stepwise multiple regression of landscape variables on Willow Flycatcher nest success.

Variable	Coefficient (β)	*t*	*p*
CANCOVRsd	-0.56	-5.46	<0.001
FLOODPLAIN	-0.50	-4.92	<0.001
AREA	-0.27	-2.83	0.011
TOT10-30	-0.15	-7.02	<0.001
ESTBAave	1.08	6.44	<0.001
CONSTANT	0.93	8.68	<0.001

Bivariate correlations. – Two landscape variables related to patch dimensions were significantly and positively correlated with brood parasitism rates: patch area and average width (Table 7). The positive correlation coefficients indicate that with increasing patch size and width, brood parasitism rates increased. This result is opposite what would be expected if these riparian woodland patches showed an edge effect.

An additional three variables showed not-quite-significant trends as well. Parasitism rates increased with the number of small stems (10-30cm DBH), but decreased with increasing stems in the 30-50 cm DBH size class and with the percentage of boxelder.

Multiple regression analysis. -- The average patch-wise rate of cowbird parasitism was best predicted by a single variable in a stepwise multiple regression analysis. The average parasitism rate decreased with increasing percentage of boxelder ($r^2 = 0.21$, $F_{1,23} = 6.04$, $p = 0.022$). This model explained only about 20% of the variation in parasitism rates among patches.

DISCUSSION

What constitutes Willow Flycatcher habitat at the patch level?

Patch occupancy. – Within the circumscribed area of the Cliff-Gila valley, we noted a wide range in density of Willow Flycatchers, including numerous patches with no birds at all. At a basic level, the birds occupied only the more mature, taller, and more structurally complex patches. We ignored the younger, simpler patches in our analyses.

Among those older, more complex patches, flycatchers showed distinct preferences for larger, longer patches with a higher proportion of boxelder, relatively lower variation in the density of shrubs, and those closer to water and to the next nearest patch. Most of these variables are partially correlated with each other. For example, boxelder tends to be more frequent in patches closer to water. In part because of these correlations, a logistic regression model identified only three variables as significant predictors of patch occupancy: boxelder, distance to the next nearest patch, and variation in shrubs. The model successfully categorized a higher percentage of occupied (96%) than unoccupied patches (78%). This may reflect the fact that occupied patches varied less in the various measurements than did unoccupied patches. It may also mean that some occupied patches (those incorrectly categorized as occupied) are in fact suitable for flycatchers, but have not yet been colonized. Thus, the area may not be saturated with flycatchers yet.

Table 7. Bivariate correlations of landscape variables with average patch-wise rates of brood parasitism in Willow Flycatchers

VARIABLE	Pearson *r*	*p*
AREA (ha)	0.43	**0.027**
LENGTH (m)	0.14	0.49
AVEWIDTH (m)	0.41	**0.032**
LENGTH/WIDTH	-0.010	0.62
PERIMETER/AREA	0.021	0.92
CANCVRave (%)	-0.26	0.21
CANCVRsd	-0.11	0.61
CANHTave (m)	-0.30	0.14
CANHTsd	-0.24	0.24
SHRUBave (count)	0.14	0.50
SHRUBsd	-0.16	0.46
TREESave (count)	0.30	0.14
TREESsd	0.046	0.83
Stems10-30 (count)	0.38	0.053
Stems30-50 (count)	-0.36	0.069
Stems50-70 (count)	-0.31	0.12
Stems70+ (count)	-0.16	0.44
%BOX	-0.38	0.054
%SALIX	-0.13	0.54
BASALAREAave (m^2)	0.13	0.52
BASALAREAsd	-0.015	0.94
DistH20 (m)	0.12	0.54
DistRIVER (m)	0.11	0.60
DistNEAREST (m)	0.014	0.94
DistOCCUP (m)	-0.15	0.45
FLOODPLAIN (m)	0.11	0.59
UPLAND (m)	0.13	0.53
DistROAD (m)	0.037	0.85

Previous studies of this population of flycatchers have shown that boxelder is strongly preferred for nesting (Stoleson and Finch 1999a, b). Therefore, it seems logical that patches with an abundance of the preferred nesting tree would be more likely to have flycatchers than those without. The second variable, distance to nearest patch, suggests that flycatchers are more likely to colonize and occupy habitat patches that are near other habitat patches rather than isolated. Perhaps the likelihood of flycatchers dispersing among patches decreases with distance between patches, as has been shown with other birds (Greenwood and Harvey 1982). Finally, although occupied and unoccupied patches did not differ significantly in the average number of shrubs per sample point (Table 2), occupied patches had considerably less variation within the patch. This suggests that Willow Flycatchers tended to avoid the extremes of very dense undergrowth and very open understory. Although often thought of as a shrub-inhabiting bird, the flycatcher's weak feet and short legs make it unsuitable for hopping through dense thickets. At the other extreme, very open understories may provide inadequate cover from predators or substrates for insect prey.

Population density. – Not only was the proportion of boxelder a significant predictor of patch occupancy, but it was the sole variable found to be significantly correlated with flycatcher density. This too can be attributed to the strong preference birds in this population show for nesting in boxelder.

What patch and landscape-level factors affect Willow Flycatcher nest success and brood parasitism?

Nest success. – Assessing correlates of nest success based on a per-patch average is necessarily a coarse-level analysis for a variety of reasons. Habitat within patches may vary, as may the ability for observers to locate and monitor flycatcher nests. Most nest failures in this population result from predation (Stoleson and Finch 1999a). Therefore, any factors we identify as significant correlates of nest success may in fact be irrelevant to the flycatcher itself, but instead may represent correlates of density of the particular suite of predators found at the site. However, even if that were the case, our findings remain relevant for at least this site.

We identified a variety of variables that were significantly associated with nest success in both bivariate and multiple regression analyses, although the two analyses found different sets of correlates (Tables 5 & 6). Generally, nest success tended to be higher in more mature patches: those with taller and more closed canopies, more trees in the larger size classes (and so higher basal area), and fewer trees in the smallest size class. Bivariate regressions suggested that nest success tended to increase with distance from the nearest occupied patch, though any biological explanation for such a relationship is unclear. As nearest occupied patch was not found to be a significant predictor of patch-wise nest success in the logistic regression analysis, its inclusion in the bivariate may be an artifact of this particular data set or completely spurious. Equally inexplicable was the inclusion in the logistic regression of both patch area and floodplain width, both negatively correlated with nest success. Perhaps larger patches, or patches in wider floodplains, were more likely to be used as hunting grounds for the major avian predators at the site (Cooper's Hawk *Accipiter cooperii*, and Common Raven *Corvus corax*). Further work is needed to verify and understand these relationships.

Brood parasitism. – As with nest success, the patch-wise rates of brood parasitism were associated with different variables in the bivariate and multiple regression analyses. The bivariate analyses suggested that as patch width, and so area, increased, so did average parasitism rates. Why this might be so is unclear, as it seems contrary to patterns reported from fragmented forests in the Midwest and Eastern states (Robinson et al. 1995). One possible explanation is that like other flycatchers, Willow Flycatchers demonstrate conspecific attraction – that is, birds tend to be clumped in distribution across a landscape. Anecdotal information suggests that dispersing birds, especially young birds, are most likely to settle close to other flycatchers whenever possible, rather than cuing in to any particular aspect of the habitat itself (Muller et al. 1997). By doing so, larger clusters of flycatchers in larger patches are more likely to include many young, inexperienced birds occupying less suitable or marginal microhabitats within the patch. These inexperienced birds are most likely to be the ones parasitized or depredated. Such a pattern was documented in Hooded Warblers (*Wilsonia citrina*; Stutchbury 1997).

Based on the logistic regression analysis, boxelder was the only significant predictor of patch-wise parasitism rates. With an increasing proportion of boxelder, patch parasitism rates

tend to decline. This result may help to explain why these flycatchers prefer boxelder as a nesting tree. In previous analyses at the scale of nest site, we found that nests in boxelder were much less likely to be parasitized than were nests in either willows or Russian olive, the next most frequent nesting substrates in this population (Stoleson and Finch in review).

Landscape-level Processes in a Linear Riparian Ecosystem

Evidence for edge effects. – Edge effects are best recognized at the scale of individual nests, rather than whole patch. However, as narrower patches have a greater portion of their area close to edges than do wider patches, any correlate of patch width could be considered an indication of an edge effect. Patch width was significantly correlated only with brood parasitism, and that was a positive correlation: the wider the patch, the higher the average parasitism rate. This contrasts with the predicted pattern if edge effects pertained to this system. In previous analyses at the nest site scale, we found no significant differences in distance to edge between successful and failed nests, or between parasitized and nonparasitized nests, supporting our finding reported here of no evidence for edge effects (Stoleson and Finch 1999a).

Evidence for patch size effects. – Although larger patches were more likely to be occupied by flycatchers, we found no data to indicate that patch size affected Willow Flycatchers in the same way it affects forest interior species in the East. Our analyses suggest that average rates of nest success actually decrease with patch size, and that brood parasitism rates increase with patch size – both opposite to the usual conception of patch size effect. Willow Flycatchers in the Southwest occur in habitat that is naturally patchy, so it was expected that we found no negative impact of small patch size. However, the opposite effect, of apparent benefit from smaller patches, is unexpected. As mentioned above, this apparent inverse effect may result from conspecific attraction.

Management Implications

Apparent Impacts of Grazing. – Although grazing has been identified as a major causal factor for the decline and endangerment of the southwestern Willow Flycatcher (Marshall and Stoleson 2000), we found no significant negative impact of grazing on flycatcher nest success or brood parasitism in this system. In fact, grazing was associated with a higher likelihood of patch occupancy and higher densities of flycatchers. It seems unlikely that this association actually reflects a causal relationship, however.

We feel the reason for this apparent paradox is the type of grazing management practiced at our site, compared to that practiced in most areas of the Southwest. Almost all of our grazed patches are part of the U Bar Ranch, which practices a very progressive management style based on rapid rotations and adaptive management. They employ no fixed rotation schedules, and those patches that are grazed support cattle only in fall and/or winter, and then for brief periods (D. Ogilvie, manager U Bar ranch, personal communication). Therefore, our assessment of grazing impacts is unlikely to apply to other grazing management practices. The type of management practiced by the U Bar is becoming increasingly common, however (Ehrhart and Hansen 1997, Leonard et al. 1997).

Importance of boxelder. – It should be apparent that the one factor most significantly and strongly associated with Willow Flycatcher occurrence and success in the study area is the prevalence of boxelder. This tree species seems to define good flycatcher habitat both at the nest site and patch levels. Our study site is unusual among Southwestern Willow Flycatcher sites in the use of boxelder, primarily because most of this tree's range lies well above the elevations where the flycatcher is most frequently found. Further, boxelder is most common along steep-sided, high-gradient montane streams, which are unsuitable for Willow Flycatchers. Thus, our findings concerning boxelder may be mostly irrelevant to most other active or potential Willow Flycatcher sites in the Southwest.

However, our results may be very important within this valley, and in other floodplain riparian areas at similar or higher elevations. In these mid-elevation areas, flycatchers may benefit from management that actively promotes boxelder. Boxelder is a secondary-successional, shade-tolerant species that may become established only slowly, if ever, in

disturbance-prone sites. Based on the analyses presented here, the Gila National Forest in 2000 began "head-starting" the successional process in their Gila Bird Habitat Management Area by planting several thousand boxelder saplings in young cottonwood-willow stands there, with the goal of attracting more flycatchers to the area.

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REFERENCES

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64: 912-923.

Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267: 1956-1957.

Danielson, W. R., R. M. DeGraaf, and T. K. Fuller. 1997. Rural and suburban forest edges: effect on egg predators and nest predation rates. Landscape and Urban Planning 38: 25-36.

Ehrhart, R. C., and P. L. Hansen. 1997. Riparian Technical Bulletin, No.3: Effective cattle management in riparian zones: a field survey and literature review. Missoula, MT, USDI Bureau of Land Management.

Freemark, K. E., J. B. Dunning, S. J. Hejl, and J. R. Probst. 1995. A landscape ecology perspective for research, conservation, and management. Pp. 381-427 *in* Ecology and management of Neotropical migratory birds (T. E. Martin and D. M. Finch, Eds.). New York, Oxford University Press.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13: 1-21.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100: 272-284.

Leonard, S., G. Kinch, V. Elsbernd, M. Borman, and S. Swanson. 1997. Technical Reference, 1737-14 1997: Riparian area management: grazing management for riparian-wetland areas. Denver, CO, USDI, Bureau of Land Management.

Marshall, R. M. 2000. Population status on breeding grounds. Pp. 3-11 *in* General Technical Report, RMRS-GTR-60: Status, ecology, and conservation of the southwestern willow flycatcher (D. M. Finch and S. H. Stoleson, Eds.). Ogden, UT, USDA Forest Service, Rocky Mountain Research Station.

Marshall, R. M., and S. H. Stoleson. 2000. Threats. Pp. 13-24 *in* General Technical Report, RMRS-GTR-60: Status, ecology, and conservation of the southwestern willow flycatcher (D. M. Finch and S. H. Stoleson, Eds.). Ogden, UT, USDA Forest Service, Rocky Mountain Research Station.

Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Missoula, Biological Resources Division, Montana Cooperative Wildlife Research Unit, University of Montana.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150: 650-661.

Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology 8: 17-26.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1990.

Rourke, J. W., T. D. McCarthey, R. F. Davidson, and A. M. Santaniello. 1999. Nongame and Endangered Wildlife Program Technical Report, 144: Southwestern Willow Flycatcher nest monitoring protocol. Phoenix, AZ, Arizona Game and Fish Department.

Sogge, M. K., and R. M. Marshall. 2000. A survey of current breeding habitats. Pp. 43-56 *in* General Technical Report, RMRS-GTR-60: Status, ecology, and conservation of the

southwestern willow flycatcher (D. M. Finch and S. H. Stoleson, Eds.). Ogden, UT, USDA Forest Service, Rocky Mountain Research Station.

Sogge, M. K., T. J. Tibbitts, and J. R. Petterson. 1997a. Status and breeding ecology of the Southwestern Willow Flycatcher in the Grand Canyon. Western Birds 28: 142-157.

Sogge, M. K., R. M. Marshall, S. J. Sferra, and T. J. Tibbitts. 1997b. National Park Service Technical Report, NPS/NAUCPRS/NRTR-97/12: A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol.

Stoleson, S. H., and D. M. Finch. In review. Breeding bird use and nesting success in exotic Russian olive (*Elaeagnus angustifolia*) in New Mexico. *Wilson Bulletin*.

Stoleson, S. H., and D. M. Finch. 1999a. Reproductive success of Southwestern Willow Flycatchers in the Cliff-Gila Valley. Summary report on the 1998 field season. USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM.

Stoleson, S. H., and D. M. Finch. 1999b. Unusual nest sites for Southwestern Willow Flycatchers. Wilson Bulletin 111: 574-575.

Stoleson, S. H., D. M. Finch, and H. A. Walker. 1998. Surveys for southwestern willow flycatchers along the Gila and Mimbres Rivers, New Mexico: Final Report. Albuquerque, NM, USDA Forest Service, Rocky Mountain Research Station, (unpublished report to The Nature Conservancy).

Stoleson, S. H., J. Agyagos, D. M. Finch, T. D. McCarthey, J. C. Uyehara, and M. J. Whitfield. 2000. Research needs. Pp. 119-127 *in* General Technical Report, RMRS-GTR-60: Status, ecology, and conservation of the southwestern willow flycatcher (D. M. Finch and S. H. Stoleson, Eds.). Ogden, UT, USDA Forest Service, Rocky Mountain Research Station.

Stutchbury, B. J. 1997. Effects of female cowbird removal on reproductive success of Hooded Warblers. Wilson Bulletin 109: 74-81.

Szaro, R. C. 1989. Riparian forest and scrubland community types of Arizona and New Mexico. Desert Plants 9: 70-138.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79: 2890-2903.

Trexler, J. C., and J. Travis. 1993. Nontraditional regression analyses. Ecology 74: 1629-1637.

Whitfield, M. J. 1990. Willow flycatcher reproductive response to Brown-headed Cowbird parasitism. Masters Thesis, California State University, Chico, California.